# YUCCAS AND YUCCA MOTHS—A HISTORICAL COMMENTARY[1]

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ABSTRACT

The famous yucca–yucca moth pollination mutualism is presented in simplified, idealized form in most biology text books and some books on pollination biology itself. In fact, the interaction is probably more complicated than any single account has implied. It was first noticed in 1872 by George Engelmann but worked on much more by entomologist C. V. Riley and botanist W. Trelease. A conventional statement of the sequence of events is given and the complications are considered. References to seed setting in the absence of *Tegeticula* are reported that may be due to self-pollination or to the activities of other flower visitors. A nectar reward is provided by septal nectaries at the base of the ovary in many species of *Yucca*. There is disagreement among authors as to whether plants of some species are self-compatible and as to the extent of geitonogamy in various species. *Tegeticula yuccasella* appears to be the pollinator of all yucca species east of the Rockies and all the western species except *Yucca whipplei* (sensu lato) and *Y. brevifolia*. *Yucca whipplei* is served by *Tegeticula maculata*, which is diurnal in operation and has to contend with a capitate stigma. *Yucca brevifolia* also has its own species of yucca moth (*T. synthetica*). Natural hybridization appears to be rampant in the species pollinated by *T. yuccasella* but not for the two western species that have separate *Tegeticula* pollinators. There is some evidence, however, that *T. yuccasella* is a complex of taxa separately adapted to individual species of *Yucca*. Another genus is concerned with the pollination in Arizona and southeastern Mexico: *Parategeticula*, which has very different oviposition and larval behavior. "Tentacleless" *Tegeticula* occur in significant proportions in some populations and, like the "bogus yucca moths," they are purely parasitic, not displaying any pollinatory activities. An attempt at placing these organisms in an evolutionary context is made.

It is interesting that in pollination biology and other disciplines significant biological discoveries become increasingly simplified in the telling and retelling of the story in text books and the general biological literature, even as the actual process is discovered to be increasingly complex. Thus, the pollination biology of the 35 or 40 species of *Yucca* is widely quoted as a unique example of strict mutualism—the yucca being entirely dependent on the yucca moth for pollination and the moth being totally dependent on some of the developing yucca seeds for the nourishment of its larvae.

The relation of the yucca moth to the yucca plant has especial relevance to us in that it was first seen by the man honored by this symposium—Dr. George Engelmann. Notes on file at the Missouri Botanical Garden referring to the pollination of yucca plants include those made by Dr. Engelmann in 1872.

> 1872. June 13th . . . .
>
> I see many insects about the flowers, bees bumblebees and others, but principally a white moth of the alliance of *Tortrix* [crossed out] *Tinea* often two (a pair!) in one flower, which fly at dusk, but are quickly [?] hid in the flower in day time.
>
> They seem to transport the pollen into the stigmatic tube . . . .
>
> July 16th. Capsules very much constricted, remain small, none full grown. Today [I] observed the first holes in them, where a larva of our [?] moth has gnawed through and escaped (into the ground?). Opening a capsule I find 4 or more larvae in it and almost all the seeds eaten up.
>
> In the first days of July *Mr Riley* found the Yucca in full bloom in Kirkwood [Missouri], fertilized by the moth—which by a peculiar appendage of the mandible (peculiar to the female, wanting in the male) gathers up the pollen, pushes it into the stigmatic tube and lays its egg (into it-no). [Parentheses and "no" added later in pencil.]

In the Bulletin of the Torrey Botanical Club for July 1872, Engelmann (1872a) reported the

[1] I am grateful to B. L. Mykrantz, archivist at the Missouri Botanical Garden, for photocopies of correspondence by Engelmann and Riley, and to G. Davidse for inviting me to contribute to the symposium and for much help with logistics. I thank J. Powell for much good advice and the use of his photograph of *Tegeticula*, D. Davis for giving permission to reproduce his drawing of *Parategeticula*, and L. Heckard for permission to use photographs in the Jepson Herbarium collection at U.C. Berkeley. Irene Baker assisted in every possible way.

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pollination of yucca flowers by a white moth of the genus *Tortrix*. Subsequently, he protested that he had written "allied to *Tortrix*" (Engelmann, 1872b).

But it was Dr. Charles V. Riley, the Missouri State Entomologist, who worked for over 20 years on the pollination biology and systematics of the moths involved and their relatives, continuing the work he began in Missouri when he became Chief of the Entomology Division of the U.S. Department of Agriculture. His first account was delivered at a meeting of the American Association for the Advancement of Science at Dubuque, Iowa, which was picked up by the British journal "Nature" in August 1872 (Anon., 1872). Riley wrote many papers on the mutualism (e.g., Riley, 1872, 1881, 1892, 1893). A full listing of Riley's papers is given by Davis (1967). Contributions were also made by Dr. William Trelease, Director of the Missouri Botanical Garden (Trelease, 1893, 1902). Coquillet (1893) observed the pollination of *Yucca whipplei* in California. In the older references the moth genus is given as *Pronuba,* but that name was shown to be invalid and has been replaced by *Tegeticula* (Davis, 1967).

## Yucca–Yucca Moth Mutualism

What is the marvellous story as described by Riley?

The female moth emerges from a pupa in the ground near a yucca plant and mates in the yucca flower with a male (who plays no part in the pollination process). She (Fig. 1) flies nocturnally to a freshly opened *Yucca* flower and with specially adapted mouthparts (including "tentacles" on the maxillae, Fig. 2), scrapes pollen from the anthers and forms it into a ball that she carries between the "tentacles" and her thorax (Fig. 3).

Then she supposedly flies to another plant and, finding a suitably receptive flower, she enters it and, aligning herself appropriately, with her ovipositor she penetrates the ovary wall and lays a thread-like egg in one of the locules in the superior ovary. Then she clambers from the base of the flower (actually often uppermost because the flowers are frequently pendulous) to a position from which she can place some or all of her pollen load in the tube that is formed by the separated ends of the fused styles (Fig. 4). She rams the pollen into this stigmatic groove (which is lined with papillae and exudes a stigmatic exudate). Pollen could not easily get there without the aid that she gives it. But the yucca moth does not feed at all.

There may be repeat performances of egg-laying by the moth so that several locules of the ovary will receive eggs. But, with the pollination achieved, the food supply of the larva (the developing seeds) is assured, while not all of the seeds are destroyed and the survivors are available to perpetuate the yucca species.

There are six locules in the ovary and each may receive one or more eggs. The larvae consume seeds in their immediate vicinity and the fruit shows a constriction in the region of a larva. The larva bites a hole in the fruit wall when it reaches the right state of maturity and descends to the ground either on a silken thread (Riley, 1892) or more likely simply by dropping (Davis, 1967). Entering the soil it forms a cocoon and rests until an environmental signal causes it to pupate and shortly afterwards, the adult emerges and the stage is set for the annual re-enactment of the interaction. The timing of the emergence is closely correlated with the flowering of the yucca.

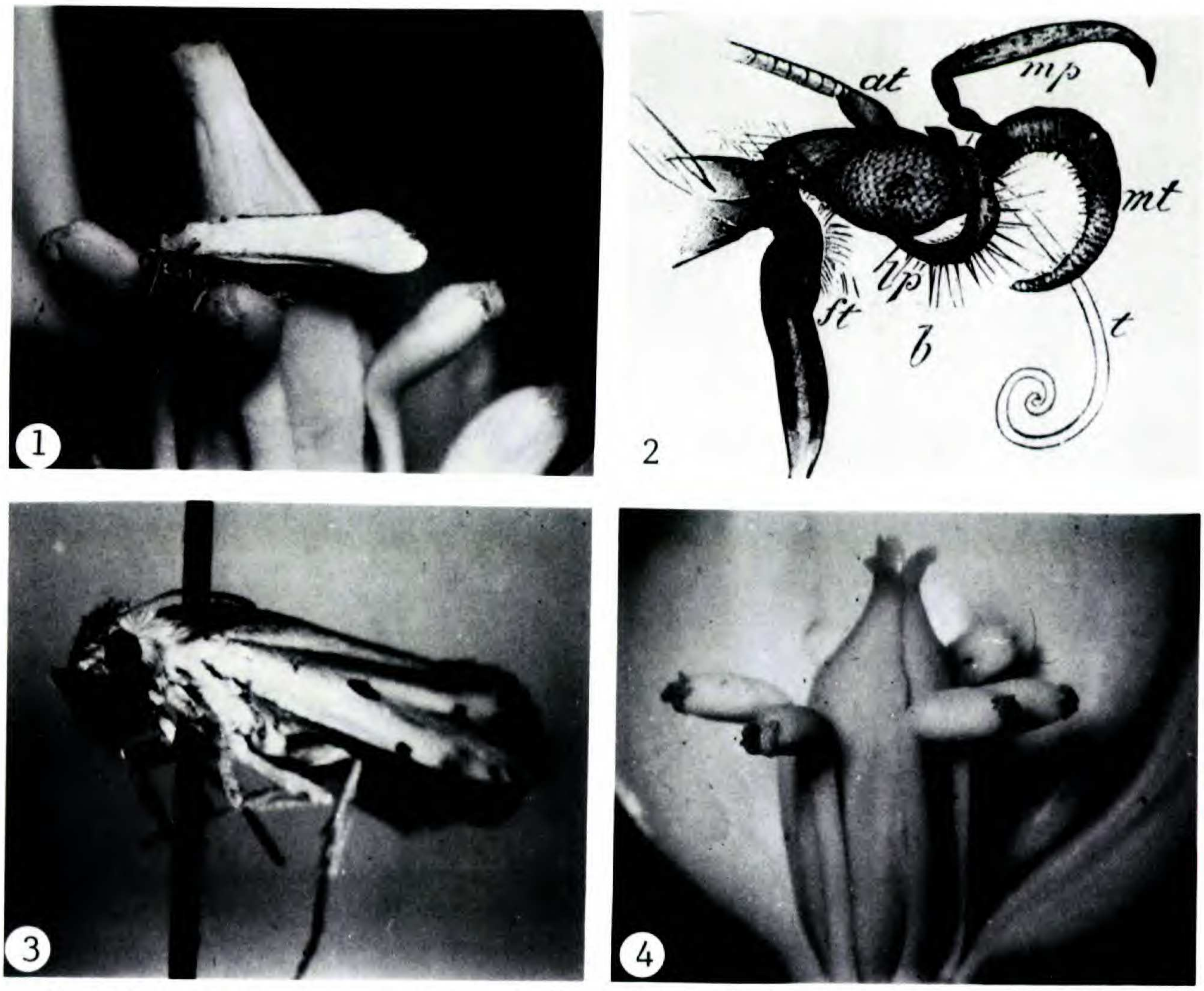
Correspondence on file at the Missouri Botanical Garden indicates that Riley sent cocoons of *T. yuccasella* to at least five persons in charge of ornamental yucca plantings in Europe and in Massachusetts, where the moth does not occur naturally, to see if the moths would emerge and pollinate these yuccas. Unfortunately, we do not know if they were successful experiments. Possibly the timing of emergence would not be correct in the new environments.

Galil (1973) has suggested that the apparently purposeful pollinatory activity of the yucca moth deserves recognition as "ethodynamic" pollination as opposed to the conventional "topocentric" pollination (depending upon the relative positions of anthers and stigma, with pollination clearly mechanical). Only *Ficus* provides other known cases of ethodynamic pollination.

## Complications

In the text books this story is held to be a valid generalization for all yuccas and yucca moths. But careful reading of first-hand accounts that have been published reveals that the true situation may be more complicated. Some field reports suggest that other potential pollinators visit *Yucca* and further, seed set may occur without pollinator intervention.

Wiggins (1980: 834), in his flora of Baja Cal-




FIGURES 1–4.—1. Female yucca moth (*Tegeticula synthetica*) in flower of *Yucca brevifolia*. Photo by C. S. Webber in the Jepson Herbarium, University of California, Berkeley.—2. Side view of head of yucca moth (*T. synthetica*) showing one maxillary palpus (mp) with its "tentacle" (mt) as well as the base of the antenna (at), eye (e), front trochanter (ft), labial palpus (lp), bristle (b), and proboscis (t). From Riley (1892).—3. Female yucca moth (*T. maculata*) with ball of pollen. Photo by J. Powell.—4. Half flower of *Yucca brevifolia* showing carpels separated at apex, producing the stigmatic groove. Photo by C. S. Webber in the Jepson Herbarium, U.C.B.

ifornia, noted that "All of the yucca species are attractive plants. Their flowers are delicately fragrant and attract bees, wasps, moths and beetles." But we do not know which of these are effective pollinators. It is frequently stated that the yucca has no possible pollinators besides the yucca moth, although reports of seed-setting by yuccas not serviced by yucca moths appeared as early as 1892 in a note to the Torrey Botanical Club by "J.W.B." of Flushing, Long Island (probably J. W. Barstow), who mentioned that "In my own garden, the *Y. filamentosa* Gray, blooms and matures its seed annually. I have never been able to discover the intervention of any insect to assist fertilization, nor have I ever failed to secure the prompt germination of seed taken from any well-matured capsule." The same species, *Yucca filamentosa*, was cultivated in Israel by Jacob Galil. He reported (Galil, 1973) that "In *Y. filamentosa* spontaneous fruit set is never encountered in the garden" but Galil did find this to occur in *Yucca aloifolia*, which was also cultivated there. This he attributed to the action of honey bees. He is one of the few authors who have drawn attention to the fact that most yuccas have some nectar secretion from septal nectaries on the ovary. This may be quite voluminous in some species (e.g., *Y. guatemalensis* and *Y. elata*, Trelease, 1893).

There is also a more or less abundant stigmatic secretion that could serve as a reward to flower-visitors as it contains sugars (Horowitz et al., 1972). It is most abundant in *Yucca aloifolia*. In Israel, Galil (1973) pointed out that cultivated plants of both *Y. aloifolia* and *Y. filamentosa* are self-compatible, in contrast to the conclusion by East (1940) that these species are self-incompatible. Trelease (1893) also referred to the frequent fruiting of *Y. aloifolia* without *Tegeticula* pollination.

TABLE 1. Infra-generic classification of Yucca (35–49 spp.).

| | | | |
|---|---|---|---|
| I | SARCOCARPA | fleshy fruit; lobed stigma | a number of spp. |
| II | CLISTOCARPA | spongy fruit; lobed stigma | *Y. brevifolia* |
| III | HESPEROYUCCA | dehiscent capsule; capitate stigma | *Y. whipplei* (s.l.) |
| IV | CHAENOCARPA | dehiscent capsule; lobed stigma | a number of spp. |

"Spontaneous" seed-setting was also found by Webber (1953) in *Yucca whipplei* and, at least, self-compatibility (though not necessarily self-pollination) in some populations of this species has been commented upon by several other authors (e.g., McKelvey, 1947; Wimber, 1958; Powell & Mackie, 1966; Aker, 1981, 1982a, 1982b). These authors concluded that self-pollination in this species was uncommon. Webber (1953: 67), based on years of collecting and observing yuccas in the southwestern states, wrote:

> Outside of *Y. brevifolia* and *Y. whipplei,* our southwestern yuccas are not reproducing to any extent by seeds. There can be little question, therefore, that the yucca moth is more dependent on the yucca for its existence than the yucca is on the moth. During their long life, through vegetative reproduction, the majority of yuccas would continue to exist for many years without the moth. On the other hand, it appears that the yucca moth would be completely wiped out if the yuccas failed to flower for a single year.
>
> Regardless of the fact that yuccas are about equally self- and cross-fertile and that the moth flies from flower to flower, it is doubtful if cross-pollinations are as prevalent as reported. It is very likely that the number of self-pollinated flowers far exceeds the number of cross-pollinated ones, and except in areas where species are admixed and flower at the same time interspecific crossing is but remotely possible.

This view is possibly too extreme but the situation does require further study. Apparently, Webber was not correct in assuming that all the moths in the soil would emerge the next year. Aker (1981, 1982a) pointed out that the emergence may be spread over three years.

## A Plurality of Yucca Moths

Botanists too easily refer to insects by all-inclusive names—like "the bee" and "the ant." So it is with *the* yucca moth. Actually, there are at least four species of pollinating yucca moth (and even two genera). Thus, *Tegeticula yuccasella* seems to be the pollinator of all the *Yucca* species east of the Rocky Mountains and of all the western species except *Yucca whipplei* (in the wide sense) and *Yucca brevifolia,* which have their own species of *Tegeticula* (McKelvey, 1938, 1947). This fits with the generally accepted systematics of the genus *Yucca* (Trelease, 1902) where four sections are recognized if the genus is not split (Table 1).

*Yucca whipplei* is so different in several morphological, physiological, and ecological features that it has been suggested that a separate genus *Hesperoyucca* be set up to accommodate it (J. G. Baker, 1892). Consequently, it is not surprising that it has a separate species of yucca moth, *Tegeticula maculata* (Table 2), which can operate in the daytime and which has to smear pollen (which is stickier than in other yuccas) on a capitate stigma instead of ramming it into a stigmatic groove (Fig. 5). Several twentieth century studies of the pollination of *Yucca whipplei* have been made (McKelvey, 1947; Webber, 1953; Wimber, 1958; Powell & Mackie, 1966; Udovic, 1981; Aker, 1981, 1982a, 1982b; Udovic & Aker, 1981; Aker & Udovic, 1981) and its pollination biology is probably better known than that of any other species of *Yucca.*

*Yucca whipplei,* including *Y. peninsularis* and *Y. newberryi,* has at least six morphologically distinct subspecies (Haines, 1941; Epling & Haines, 1957). Its *Tegeticula* (*T. maculata*) has a melanic subspecies (subsp. *extranea*) as well as the type subspecies (subsp. *maculata*).

*Yucca brevifolia,* the Joshua tree, is the only species with a "papery" or "spongy" fruit. It has a yucca moth, *Tegeticula synthetica* (also known as *T. paradoxa*) entirely to itself (Table 2) (McKelvey, 1947; Davis, 1967).

## Timing and Moth Emergence

Powell and Mackie (1966) showed that *Yucca whipplei* flowers may be available for two to three months, so precise timing of the emergence of the moth is not essential for this species. However, in other species this does seem to be precise

TABLE 2. *Tegeticula* species associated with sections of the genus *Yucca*.

| | |
|---|---|
| SARCOCARPA<br>CHAENOCARPA | *Tegeticula yuccasella* |
| CLISTOCARPA | *Tegeticula synthetica* |
| HESPEROYUCCA | *Tegeticula maculata* |

and Rau (1945), who made sustained observations at Kirkwood (the place in Missouri where the mutualism was first investigated) found evidence that temperature was an important controlling factor in the coincidence of flowering of *Yucca filamentosa* and the emergence of the moth. For *Yucca whipplei*, Powell and Mackie (1966) suggested that the rainfall pattern is crucial.

## HYBRIDIZATION AND SYSTEMATICS

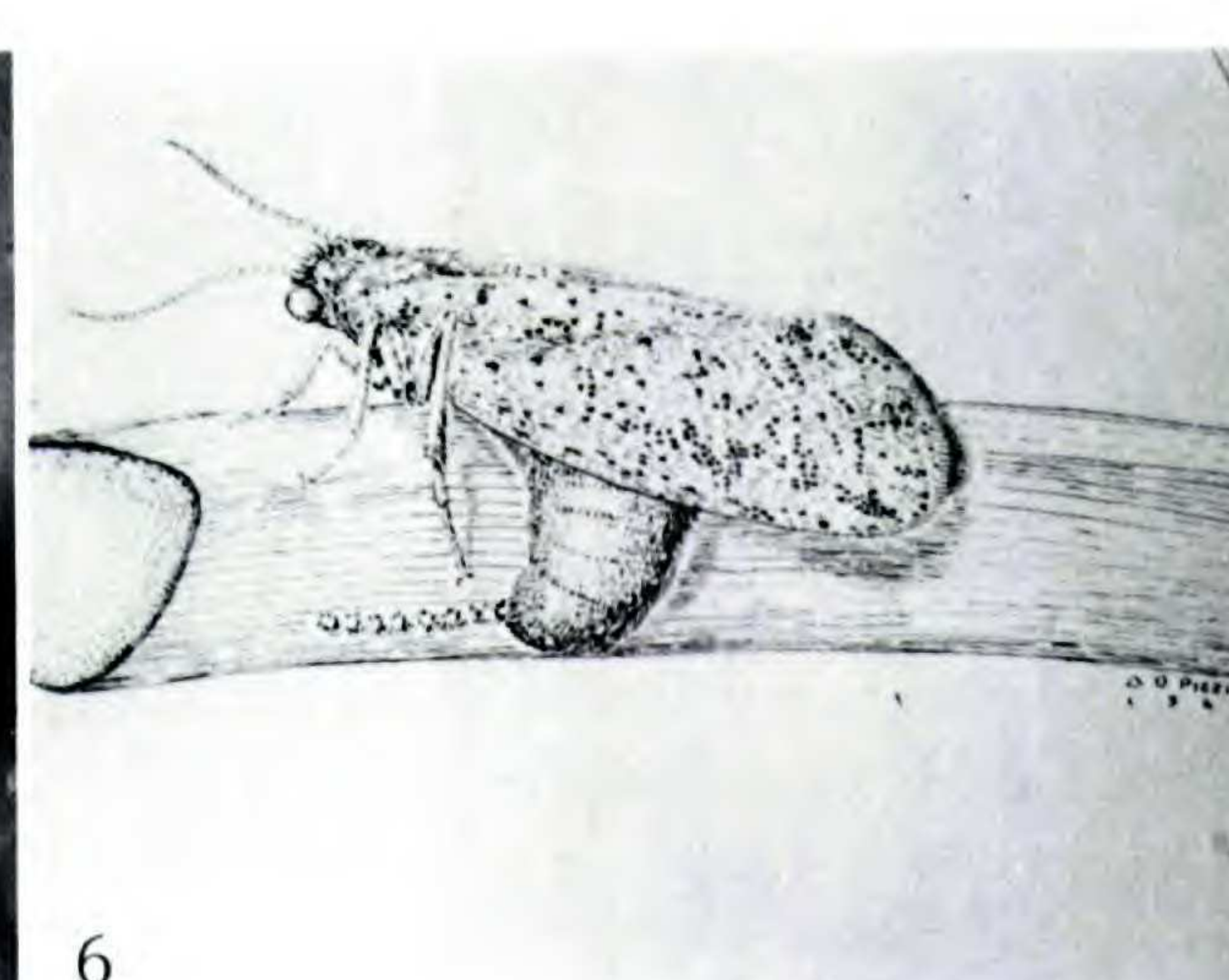
It is notable that interspecific hybridization is rampant among the species that are pollinated by *Tegeticula yuccasella*. Webber (1953) listed at least 15 combinations, and McKelvey (1938, 1947) found others. Webber (1953) and Galil (1973) have both obtained seed from artificial crosses. The gene-flow in nature may be responsible for the blurred specific boundaries between some of the species and taxonomic disagreements about species limits. But the two yucca species that have their own yucca moth species have remained free from hybridization, even where they have come into proximity to other species.

Nevertheless, there is evidence that *Tegeticula yuccasella* is not an indivisible unit systematically and ecologically. Davis (1967) seems to have been the first to suggest that all *Tegeticula yuccasella* are not alike. Particularly the variation in genitalia suggested to him that there might be distinct yucca moths associated with each of the four sections of the genus *Yucca*. We know that *Yucca brevifolia* has its own *Tegeticula*, as does *Y. whipplei*; what he suggested is that there are also distinct moths for the sections *Sarcocarpa* and *Chaenocarpa*.

In 1983, Miles carried the process further and suggested that on the basis of morphological and phenological characters shown by the moths that pollinate *Yucca baccata* and *Yucca torreyi* (section *Sarcocarpa*) and *Yucca elata* (section *Chaenocarpa*) in New Mexico, there are separate moth entities in each case, although all had been put in *Tegeticula yuccasella* in previous work. She hinted at the possibility that each yucca species has its own pollinating moth. But, I think that, in view of the widespread hybridization and blurring of specific characters in yucca east of the Rockies, the differentiation of the moths must be only at the race level rather than at the species level, with the opportunity for "mistakes" to occur with the moths pollinating taxonomically different plants than the kind that produced them. Thus, Miles (1983) found some evidence of the use of *Yucca torreyi* by moths of the *Yucca baccata* form when *Y. baccata* had finished blooming.

## *PARATEGETICULA*

I think it will come as a shock to most people that there is another genus of moth that polli-


FIGURES 5, 6.—5. Half flower of *Yucca whipplei*, with capitate, papillate-fringed stigma. Photo by C. S. Webber in the Jepson Herbarium, U.C.B.—6. Oviposition by *Parategeticula pollenifera* on pedicel of *Y. schottii*. From Davis (1967).

nates yucca, although it was described 17 years ago by Davis (1967). It was news to me when I began to assemble information for this paper, and none of the general pollination accounts published so far mention it.

The new genus is *Parategeticula* and the only species known is *P. pollenifera* (Fig. 6). It was first collected in 1959, in southeastern Arizona and subsequently, a long way away, in Veracruz, in southeastern Mexico in 1963. Davis, whose monograph on the subfamily Prodoxidae is the standard reference (Davis, 1967), went to Arizona to see it in the flowers of *Yucca schottii.* Powell (1985) has subsequently made a detailed study of this moth both in Arizona and in Veracruz (where he found it in *Yucca elephantipes*).

*Parategeticula* females have "tentacles" like *Tegeticula* and gather up pollen in a ball in the same fashion. Neither Davis nor Powell was able to see that it pollinated the stigma by actively pushing the pollen into the stigmatic cavity, but it seems reasonable to expect that it does.

*Parategeticula* then does a surprising thing. Instead of ovipositing in the ovary of the flower, it sometimes lays eggs in the fleshy petals or else in a carefully gouged line of shallow pits on the flower stalks (Fig. 6). Davis (1967) thought that it would not cause any loss of seeds to the yucca by having its larvae feed in the stem tissue, but Powell (1985) found that after development from the egg, the larva crawls up to the developing ovary and bites a hole to let itself in.

In the ovary, the larva causes degradation of the tissues of the inner side of the wall and the adjacent ovules. In the cyst that is formed, the larva then eats the distintegrated ovules. This unique larval behavior is very different from that of *Tegeticula* whose larvae develop from eggs in the ovary and wait there until the seeds are almost ripe before consuming them.

Populations of *Yucca schottii* in Arizona may have only *Tegeticula yuccasella* or only *Parategeticula pollenifera* or both at the same time (Powell, 1985). Obviously, *Parategeticula* must be looked for in more species of yucca, especially in the gap between Arizona and Veracruz.

## ALLOGAMY OR GEITONOGAMY?

It is very important to know the breeding systems of the various *Yucca* species. It seems, from the experiments of East (1940), Webber (1953), Wimber (1958), Udovic and Aker (1981), Aker (1981, 1982a, 1982b) that at least some plants of *Yucca whipplei* are self-incompatible and Webber found some self-incompatibility in six other species. Consequently, some authors have tended to take for granted that the female yucca moth regularly flies between separate plants before depositing her pollen load.

Jepson (1925: 246) wrote "The female Pronuba works by night, collecting the pollen from the anthers and rolling it into a little ball: she then flies to the flower of another plant, deposits her eggs in the ovary, and then in a manner which corresponds to actions full of purpose and deliberation climbs to the style and thrusts the pollen ball down the stigmatic tube." There is no evidence that Jepson actually saw this at first hand; the vehicle of publication being a California flora. In fact, none of the first-hand accounts justify this categorical statement that another plant is immediately sought by the *Tegeticula* moth after collecting the pollen ball.

Riley (1892) wrote "After collecting all the pollen . . . she *usually* runs about or flies to another plant; for I have often noticed that oviposition, as a rule, is accomplished in some other flower than that from which the pollen was gathered, and that cross-fertilization is thus secured" [emphasis added]. It is not clear whether the "other flower" in this quotation is more frequently in the same inflorescence than in another plant.

Trelease (in Riley, 1892: 125) wrote "Apropos of Meehan's idea that the Pronuba moth close fertilizes the flower, I have seen females when undisturbed *go from flower to flower here,* and several times in the mountains a female was seen, without having been disturbed, to fly off horizontally from a plant on the steep mountain side, with every evidence of the necessity for a long flight before finding another Yucca" [emphasis added]. This does not necessarily imply that the horizontal flight led to cross-pollination.

Webber (1953) has already been quoted as holding the opinion that more selfings take place than outcrossings. Rau (1945: 374) wrote "The moth, when ready to oviposit, gathers a ball of the sticky pollen from the anthers . . . holding it firmly under her chin she *runs* about until she finds a flower which is suitable for ovipositing" [emphasis added].

There must be inter-plant flights by the moths; the interspecific hybrids testify to this, but the evidence is circumstantial. The nearest direct evidence is provided by Aker and Udovic (1981) in the case of *Tegeticula maculata* on *Yucca whipplei,* which is easier to observe because the activity is in daylight rather than nocturnal. They wrote "In no case was a female seen ovipositing in the same inflorescence after collecting pollen. Having collected a full load of pollen the females typically crawl out on the branches or unopened flower buds, rest briefly and then fly off. In those cases where it was possible to observe them in flight, they either flew away in a straight line if there was no obstacle, or else spiralled out from the inflorescence until they were heading down wind and then flew straight. The flights were generally high, well above the surrounding vegetation, and the moths often ignored other inflorescences nearby" (Aker & Udovic, 1981: 96).

Furthermore, Aker and Udovic (1981: 97) stated "—the fact that dispersing females fly relatively long distances (i.e. tens of meters) suggests that they are minimizing the likelihood that they will return to the same plant from which they have collected pollen or visit other closely related individuals in the vicinity of the pollen donor."

Powell and Mackie (1966) do not say that they saw *Tegeticula maculata* go from plant to plant of *Yucca whipplei*. However, Powell (1985) has more recently used mark/recapture methods to show that male *Parategeticula* (the other genus) stay on one plant of *Yucca schottii* while the females go to other plants, at least sometimes.

If a plant is self-incompatible, geitonogamy will be worse than useless. Clogging of the stigma by incompatible pollen could be one cause of the tremendous voluntary shedding of fruits in *Yucca*, 50–90% according to Aker (1981, 1982a, 1982b) and Aker and Udovic (1981). They have shown that limited resources are an important cause of this and, in addition, point out that the large numbers of flowers increase the visibility of plants to the moth, and in an exceptionally favorable season there may be a higher proportion of fruits that can mature. All of these factors as well as the geitonogamy possibility may be operative.

## PARASITISM DERIVED FROM MUTUALISM

Sometimes, *Tegeticula* oviposits without pollinating. Sometimes it lays eggs in an ovary that is already developing following pollination by a previous visitor (Aker, 1981). In such cases, that particular *Tegeticula* individual is unequivocally parasitic.

This leads us to another complication. It is assumed that all the female *Tegeticula* moths are potentially capable of pollinating the *Yucca* flower but observation of collections and sampling of populations shows that this is not always so (Davis, 1967). An essential item in the pollination system is the presence on the maxillary palpus of the female moth of the "tentacles," which make possible the processing of the pollen into a ball that is carried between the underside of the mouth parts and the thorax of the moth (Figs. 2, 3).

But August Busck, who examined the many collections by Susan McKelvey (see McKelvey, 1947), pointed out that he found "20–30" out of at least a thousand specimens of female *Tegeticula* to have vestigial "tentacles" or none at all. Davis (1967) investigated this in population samples of *Tegeticula yuccasella* and found that the percentage of tentacle-less female moths could vary from zero to 71%. These tentacle-less moths apparently do not attempt to collect pollen, and if they oviposit they constitute parasites on the mutualism. It is clear that if the proportion of non-pollinators grows beyond a certain point the yucca will be less frequently adequately pollinated and it will be interesting if further quantitative analyses are made of this phenomenon and its effect on population structure in *Yucca*.

Keeley et al. (1984) discussed seed predation of nine species of *Yucca*, pointing out that in all these species, although there were some fruits in which all the seeds were consumed and some with only a proportion consumed, there were others in which no larvae were to be found. This could be due to self pollination or pollination by some other agent than *Tegeticula*, or to the failure of the moth to oviposit though it pollinated the flower. Most likely, the moth oviposited but the larvae died. They hint that some *Yucca* populations may be capable of inhibiting the hatching of *Tegeticula* eggs and thus "regulating Tegeticula densities" in their populations. However, at present, this is speculation.

## "BOGUS" YUCCA MOTHS

In addition to *Tegeticula* and *Parategeticula*, there are what Riley (1892) called "bogus yucca moths." Three genera are involved. They also are members of the Prodoxidae and oviposit in the wall of the ovary or in some part of the stem system (Powell & Mackie, 1966; Davis, 1967). They have no tentacles, and even if they visit the flowers, they do not collect pollen. Consequently they are dependent for their larval survival on the pollinating acitvities of *Tegeticula,* which causes the flowers not to be abscised and seed to be set that will result in new *Yucca* plants.

## Evolutionary History

What may be the evolutionary sequence in building the yucca–yucca moth mutualism?

In the Agavaceae, apart from *Yucca* species, pollination is topocentric (see page 557), and it is likely that a distant ancestor had this conventional pollination mechanism, which is pointed to by the production of floral nectar. When association with the Prodoxidae began (probably by the greater certainty of pollination by these moths), *Tegeticula* itself may be the starting point—an assumption that is in keeping with the universality of its association with *Yucca* as the virtually exclusive pollinator. We can either postulate that the "bogus yucca moths" evolved from *Tegeticula* with the *Tegeticula* providing the pollination for them, or some other pollinator may have been involved. The "tentacle-less" *Tegeticula* females may represent a mutant form that could show the ancestral condition. Galil (1973) considers the mutualism of *Yucca* and *Tegeticula* to be an evolutionarily rather recent event (basing this on the continued production of "useless" nectar) but the occurrence of the mutualism in all yuccas seems to point to a longer history. This is particularly the case in that *Yucca whipplei* has significant morphological differences from the rest of the genus, yet possesses *Tegeticula,* which has had time to produce subspecies, matching in distribution the subspecies of this yucca that have disjunct populations probably relict from a more continuous distribution at some time in the past (Powell & Mackie, 1966).

*Parategeticula* could be either derived from *Tegeticula* or ancestral to it. It has a distribution (admittedly not fully revealed as yet) that is within the bounds of *Tegeticula.* But it is hard to see its oviposition behavior and the movements of its larvae making a perilous journey from pedicel to ovary as an advantage over the direct oviposition into the ovary practiced by *Tegeticula* (so it might be more primitive than *Tegeticula*).

As stated above, it is notable that none of the other American genera in the Agavaceae have developed a comparable mutualism; *Agave* has many different pollinators, *Nolina* and *Dasylirion* tend to show separation of the sexes, while *Hesperaloe* may be bird-pollinated.

## Possible Parallels

As for the combination of lepidopteran pollinator and seed-predator, the only suggestive case outside of *Yucca* apparently concerns *Silene alba* (also known as *S. pratense* and *S. latifolia*), where both male and female moths of *Hadena bicruris* visit the white flowers at night in Europe (Brantges, 1976). Both staminate and pistillate flowers of this dioecious species are visited for the nectar they produce, and cross-pollination is achieved. But the female moth oviposits on the ovary in pistillate flowers and the larva eats its way into the ovary and consumes the seeds. It then moves to other flowers on the plant and consumes their seeds before descending to the ground and pupating.

Brantges (1976) has calculated that the larvae consume the contents of as many fruits as the moths had pollinated, and it is only because other non-seed predatory moths also pollinate *Silene alba* that it produces enough seed to reproduce itself (it is an annual plant). It is possible that *Silene alba* may evolve some means of curbing the appetite of the larva, in which case a mutualism of the yucca sort might be possible, but this is highly speculatory.

The simple story of mutualism between a flower and an insect is probably basically sound, but the situations in nature are being revealed to be more complex than George Engelmann had any reason to anticipate and it is to be hoped that research (observational and experimental) into this fascinating area will be stimulated by the need for more information.

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